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SUMMATION AND INHIBITION IN THE FROG'S RETINA

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Ricco's and Piper's laws relating threshold intensities and the size of a stimulus spot show that there is a mechanism in the visual pathway for summating excitatory effects from neighbouring regions of the retina. The area over which Ricco's law holds is certainly greater than the area of a single receptor cell, so the summation must be primarily neurological and not simply photochemical. Adrian & Matthews (1927*a*, *b*, 1928) and Hartline (1940*b*) showed that summation occurred if a discharge of impulses in the optic nerve was taken as the index of activity instead of the subjective sensation of light, so the neurological mechanism must lie in the retina. Spatial summation of this sort is an aspect of the activity of nervous ganglia which has been rather neglected, for obvious technical reasons; the bravest neurophysiologist would hesitate to use 1000 stimulators to excite his preparation, but the evidence indicates that a ganglion cell in the retina picks up from a region containing at least 1000 receptor cells. It was hoped that Granit & Svaetichin's (1939) type of single unit preparation in the frog's retina would provide a suitable preparation for investigating this summation, using a natural, but nevertheless easily controllable, stimulus. It was also hoped that something might emerge to indicate the reason for the large receptive fields, up to a millimetre in diameter, which Hartline demonstrated directly. The whole retina could not have an area greater than that of a hemisphere 8 mm in diameter, in which case this single fibre would be picking up from 1/128 of the whole retina. In a frog's retina there are about 30,000 nerve fibres (Breusch & Arey, 1942), and close to a million receptor cells. It would not be in the least surprising to find one fibre picking up from its fair share of receptors, but this would correspond to about thirty rods, or a circle of 0·06 mm in diameter, whereas Hartline's results suggest that one fibre connects to a circle at least ten times this size containing a hundred times as many receptors.

It is certain that there is convergence, and probable that there is overlap, in the nervous pathway leading from receptor cells to optic nerve fibres. This is reminiscent of the convergence onto ventral horn cells that occurs in the spinal cord, and Sherrington's concepts suggest that the convergence may bring about some kind of 'sensory integration'. At first sight it appears that the large amount of convergence, and the resulting overlap of neighbouring receptive fields, would 'blur' the image transmitted down the optic nerve in the same way that overlapping circles of confusion blur an optical image when the lens is defocused. Alternatively one might argue that the usefulness of the optic nerve as a communication channel would be reduced, for the overlap means that the activity of one fibre is no longer completely independent of the activity of its neighbour; certain patterns of activity become impossible, and the capacity of the channel is reduced.

The description of the action of the retina given by Hartline is surprising from a functional or teleological point of view, and the purpose of the work described here was to repeat some of his observations on convergence of activity from different retinal regions onto single ganglion cells in the frog's retina.

METHOD

Preparation. The method of obtaining action potentials from single units in the frog's retina has been described in a previous paper (Barlow, 1952). Briefly, a Granit-type electrode is placed on the retina in an excised opened eye of a frog. With a good electrode, well-placed, action potentials of 30–80 μV amplitude are obtained when the retina is excited. They are of uniform size and have the regular rhythm characteristic of single units. Preparations of this sort usually last 1 hr, occasionally 4 hr, and during this time have a fairly constant threshold.

Optical stimulator. This also was described in the previous paper. It gave an even background illumination to which was added the stimulus spot controlled by a shutter. The stimulus spot was variable in intensity, size and position. For the present work it was necessary to determine the intensities of light given by the stimulator, and this was done as follows.

(1) The preparation was replaced by a piece of matt white paper and the intensity of the constant background illumination with no neutral screens was measured with an S.E.I. visual photometer. This level of illumination was taken as the standard to which other levels were referred.

(2) A photometer eyepiece (Fig. 1) was made and fitted to a binocular dissecting microscope used for observing the preparation. This eyepiece had a thick white card with a small central hole fitted in its image plane. The card was illuminated from above, and thus on looking through it one saw a white field with a small central spot. The image of the stimulus spot in the dissecting microscope was arranged to coincide with this hole. First, however, the illumination of the top of the card was adjusted until it matched the central hole when only the background illumination of the stimulator was on. Then the background was switched off, and the stimulus spot turned on and adjusted

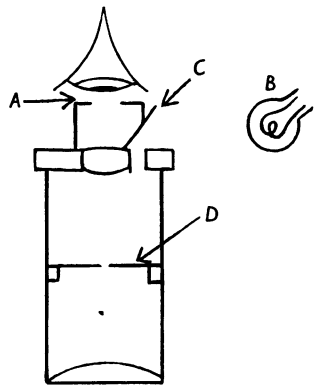

Fig. 1. Photometer eyepiece. *A*, exit pupil; *B*, lamp; *C*, reflecting surface; *D*, white card in image plane with small central hole.

in intensity with the neutral wedge until the match was re-established. This gave the setting of the wedge which produced a stimulus spot of the same intensity as the background illumination whose intensity was already known.

(3) The wedge of the stimulator was calibrated by inserting Ilford neutral filters in the path of the light, and then rebalancing as before. The neutral filters were calibrated by the makers, and this calibration was checked approximately by a photographic method. The calibration of the wedge against the filters was also checked on a frog's retina, by finding that the figure for threshold was always the same whether the stimulus light was reduced in intensity by neutral filters, by the wedge, or by combinations of the two.

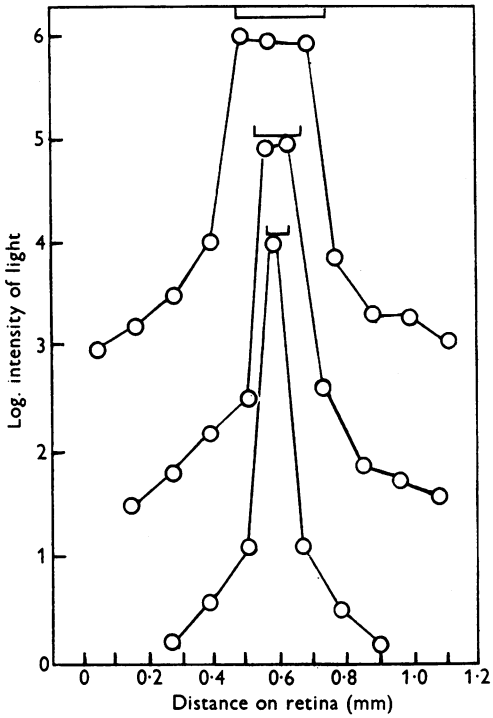

Fig. 2. Intensity of scattered light surrounding stimulus spots of three sizes; nominal diameters indicated by lines at central points. Two smaller spots are displaced downwards 1 and 2 log. units relative to largest. Intensities estimated over region 0·05 mm in diameter.

(4) The intensity of the side spot was not measured, and the results obtained when using it were referred to the threshold level for the spot on the particular preparation used.

Scattered light. The stimulator did not produce a perfectly defined image of the movable stop and the intensity of the halo of scattered light is important. The photometer eyepiece was used, to get a reliable estimate. The intensity at the centre of the stimulus spot was measured in the way already described; the stimulus spot was then moved through a measured distance and the wedge adjusted until the match was restored. In this way the level of illumination surrounding a stimulus spot was determined, and the results of runs across the centres of three stimulus spots of different sizes are shown in Fig. 2. In order to show up the fringe of scattered light the intensity is plotted on a logarithmic scale. It will be seen that the intensity has dropped to 1/100 of its peak value within 0·1 mm of the edge. Calculation based on a more extensive plot of the 0·134 mm spot showed that 97% of the light fell within a circle of diameter 0·168 mm.

It is possible that under the conditions of an actual experiment there will be some additional scattering of light in the retina itself. Unfortunately it was difficult to measure intensities around the stimulus spot when it was falling on the retina because the intensity of light reflected back to the observing microscope was less than 1/100 of that obtained with a white card. The more intense part of the spot can, however, be explored by using the eyepiece photometer at threshold level, and the results for the 0·134 mm spot are shown in the centre of Fig. 3. It will be seen that the scattered light is only slightly increased.

Procedure. A single unit was isolated, and the preparation so placed beneath the stimulator that the light fell normally on the region surrounding the electrode tip. The stimulator was then focused by placing a cross-wire graticule in the place of the movable stop and observing its image on the retina through a binocular dissecting microscope. The preparation was allowed a few minutes to recover from the rather bright illumination necessary for dissection, placing the electrode, and focusing the stimulator, and then observations of threshold under some standard conditions were taken at 5 min intervals or less until a steady level was reached. This usually took 10–20 min. The procedure for determining threshold was as follows. The shutter was opened for 1 sec every 2 sec, and the wedge was adjusted until two levels were found, one of which just gave a response whilst the other just failed. These two settings were alternated and the stronger was taken as threshold. In a good preparation a 10% reduction in intensity would lower the stimulus below threshold, but frequently a reduction of 30 or 40% was required. Whether the response occurred at the beginning or the end of the period of illumination depended on the type of unit isolated by the micro-electrode. If thresholds both for 'on' and for 'off' were needed in an 'on-off' fibre the lower threshold was taken first.

RESULTS

The results are divided into three sections. The first deals with the size of the receptive fields of the ganglion cells—that is the extent of the region described by Hartline within which incident light excites the ganglion cell. The second deals with the way in which a ganglion cell combines, or summates, effects contributed from different areas within this region. It was naturally thought that retinal areas outside the receptive field would not affect the ganglion cell, but this turned out not to be so in 'on-off' units, and experiments showing this effect are also described in the second section. The third section describes observations on the movement sensitivity of 'off' and 'on-off' units.

Size of receptive fields

Hartline (1940*a*) found receptive fields measuring up to 1 mm in diameter in the periphery of the frog's retina, and receptive fields as large as this were frequently found in these experiments if an exploratory spot many times stronger than threshold was used. In one of Hartline's experiments moving the spot from 0·19 to 0·38 mm from the centre of the receptive field raised the threshold by a factor of 10,000. Since the centre is so much more sensitive than the peripheral fringe the diameter of the central plateau is a better indication of the overlap of receptive fields and the consequent 'blurring' of the image. The sensitivity of different parts of the receptive field was therefore explored.

Fig. 3 shows how the threshold changed as the stimulus spot was moved across the centres of the receptive fields of three 'off' and three 'on-off' fibres.

Log. sensitivity (log. of reciprocal of threshold intensity) has been plotted as abscissa, and it will be seen that there is a plateau of high sensitivity 0·3–0·6 mm in diameter in all of them. Such a distribution of apparent sensitivity might be obtained if a large exploring spot was moved over a small receptive field; the distribution of light round the exploring spot is shown in the centre of this figure, and it will be seen that it might cause an increase of the apparent size of the central plateau of only the smallest receptive fields.

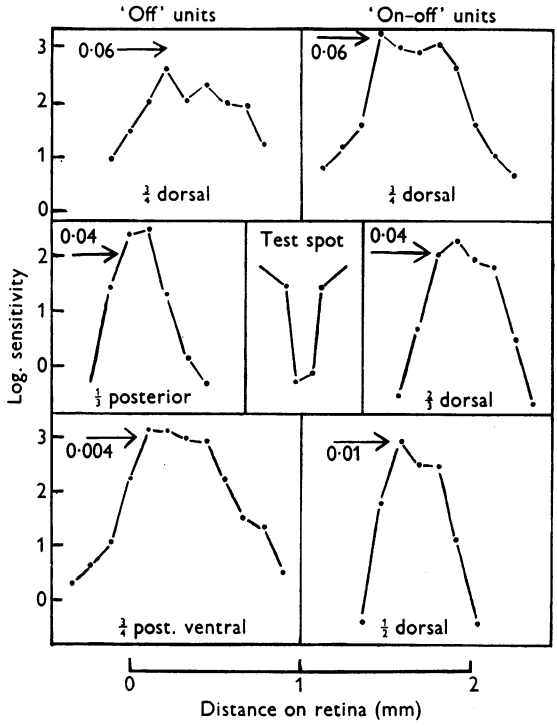

Fig. 3. Receptive fields of three 'off', and three 'on-off' units. Intensity of background in foot-candles and approximate location of unit on the retina are indicated.

The six receptive fields plotted include the smallest (middle, 'off' type), and the largest (top, 'on-off' type) that were obtained. On the whole the smaller receptive fields were found in the more central regions of the retina, and the approximate positions of those plotted here are indicated as a fraction of the total distance from optic disc to extreme periphery in the indicated direction. It was extremely difficult to isolate ganglion cells in the most central region of the retina, so that it was not possible to investigate this point further.

In each diagram the intensity of the background light is given in foot-candles, and a line is drawn to indicate the sensitivity level at which the exploring spot would have an intensity equal to the background. In most

cases the plateau does correspond to approximately this sensitivity, and in these cases the Weber fraction ($\Delta I/I$) is 1. If a larger stimulus spot were used the Weber fraction would, of course, be reduced to a more normal figure.

In addition to the type of experiment shown in Fig. 3 contours of equal sensitivity have been determined in some receptive fields, and complete maps of sensitivity in others. These showed that the fields were circular or slightly eliptical. It was remarkable how little these experiments appeared to be upset by the shadow of the electrode and the meniscus where it left the vitreous, but it is possible that some of the irregularities in sensitivity in the plateaux are the result of such disturbances.

So far this confirms Hartline's findings. The receptive fields are large—up to 1 mm in diameter in the periphery if a strong stimulus is used. They have a central plateau where the sensitivity is much higher and this varies in diameter from about 0·6 mm in the periphery of the retina down to 0·2 mm nearer the centre. There were, however, some additional findings. Fig. 4 shows the receptive field of an 'on-off' fibre from *Rana esculenta*. The threshold for both 'on' and 'off' responses was determined at each point, and it will be seen that there is no difference in sensitivity at the centre and at the extreme periphery. In the intermediate zone, on the other hand, the sensitivity for 'off' (circles) is a hundred times the sensitivity for 'on' (crosses). The reverse has also been observed in *Rana esculenta*, some receptive fields having an intermediate zone where the threshold for 'on' is lower than for 'off'. In *Rana temporaria* the thresholds for the two responses are usually closer together.

One further observation on the shapes of receptive fields was made. This arose accidentally from imperfections in an early version of the stimulator. The exploring spot of light it produced had a wide and intense flare of partially scattered light surrounding the image itself. When the receptive fields were explored in the usual manner with this stimulator, there was a definite tendency for the 'off' fibres to have a sharp peak of high sensitivity at the centre of the receptive field, whereas the 'on-off' fibres had a relatively broad, flat top. This finding could not be repeated with the improved stimulator, but it is satisfactorily explained by the inhibiting action of light falling just outside the receptive field; this affects 'on-off' but not 'off' units, and is described later in this paper.

Summation of activity within a receptive field

A ganglion cell is in functional connexion with a large number of receptor cells, and it is natural to ask how effects transmitted from these cells are summated by the ganglion cell. Hartline found that the discharge of an optic nerve fibre was determined by the quantity of light falling in its receptive field (Ricco's law). It made little difference if the light was concentrated on one or two receptor cells or if it was spread out over many. It is clear that there

must be a mechanism for summating effects from separate regions of the receptive field, even if the effects are subliminal. The present work again confirms this result for threshold stimuli, but particular attention was paid to some possible criticisms of Hartline. It is clear that the threshold must necessarily be inversely proportional to the nominal area of the stimulus spot if the spot is so small that it is not resolved by the optical system used, for

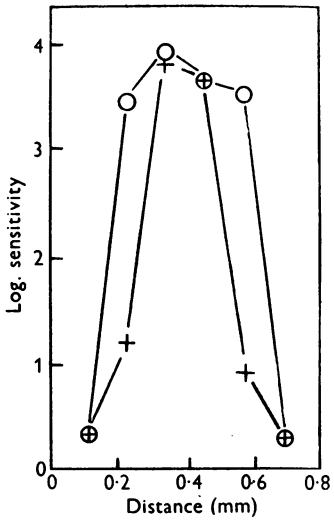

Fig. 4.

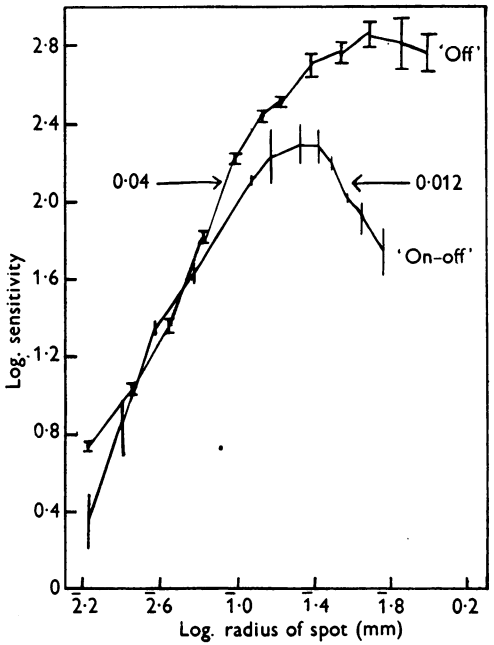

Fig. 5.

Fig. 4. Receptive fields for 'on' (crosses) and 'off' (circles) response in an 'on-off' unit from retina of *Rana esculenta*.

Fig. 5. Radius/sensitivity relation in an 'off' and an 'on-off' unit. Arrows indicate, for each curve, the sensitivity corresponding to a stimulus of intensity equal to the background, and the number gives the intensity (f.c.) of the background.

changing the nominal size would then only change the intensity of light falling on the retina, without appreciably changing the spatial distribution. This criticism would only apply to the smallest spots used by Hartline, but his largest spot had a radius of only 180 μ, and his experiments do not, therefore, prove that there is summation over the whole receptive field of the ganglion cell. The smallest spots were not used in these experiments, but the largest spots extended well beyond the receptive field, and this revealed an interesting new effect.

Fig. 5 shows the results of two experiments, one on an 'off' unit, and the other on an 'on-off' unit. Log. sensitivity (log. 1/threshold) is plotted against

log. radius of spot. Logarithmic scales are necessary because of the wide range of values covered. An arrow shows the sensitivity which corresponds to a stimulus of the same intensity as the background. Two threshold determinations were made at each radius, one set being in order of increasing size, and the other decreasing.

In this method of plotting a line of slope +2 indicates $S = 1/T \propto r^2$ where S is sensitivity, T is threshold intensity, and r is radius of stimulus spot. The early part of each curve follows this relationship fairly closely, and the deviations from it may not be more than can be accounted for by experimental error. One source of consistent error should be pointed out. The stimulus spot at small radii is sometimes almost a hundred times the intensity of the background illumination. Light-adaptation is therefore likely to occur, and the measured sensitivity will therefore be lower than it should be. It was not possible to wait longer between stimuli because of the limited life of the preparations. This type of error may be responsible for the lines tending to have a slope greater than +2. When the radius of the stimulus spot exceeds 0·1 mm the curves start deviating from each other significantly. The curve for the 'off' fibre goes on rising, at a rather slower rate, up to a radius of stimulus spot of 0·4 mm, and thereafter shows a slight tendency to fall. The curve for the 'on-off' fibre only increases up to a radius of 0·25 mm, and thereafter falls rapidly.

The similarities and differences between the curves for each type can be summarized as follows:

(1) Up to about 0·1 mm radius of spot both types require an approximately constant quantity of light for threshold.

(2) From about 0·1 to about 0·25 mm radius both types require an increasing quantity of light for threshold, but the intensity required is still decreasing.

(3) From 0·25 to 0·1 mm radius the 'off' units require an approximately constant intensity of light, but the intensity required to stimulate the 'on-off' units increases rapidly.

The same general features were usually observed, but there is quite a big variability in the points at which the curves change direction. The sensitivity of 'off' units never showed a marked tendency to decrease at large spot radii, and this has been true for all the 'off' units investigated. In some cases the slope over the initial part of the curves was much less than +2, and this was traced to faulty centering of the stimulus spots on the receptive field. Some 'on-off' units, however, showed a low slope over the early part which could not be attributed to this cause. Some of the 'on-off' units have failed to show the decrease at large radii, but a possible explanation of this is given later.

The decrease in sensitivity at large radii which is usually found in the 'on-off' units implies inhibition, whereas the curves for 'off-units' suggest only simple summation, and this type will be considered first.

'Off' units. Inspection of Fig. 5 shows that the point on the radius/threshold curve where a further increase in spot size ceases to affect the threshold intensity corresponds to a radius of 0·4 mm. This suggests that as soon as the whole receptive field is covered by the spot a further increase of spot size ceases to affect the ganglion cell. The slope of the curve starts to decline at

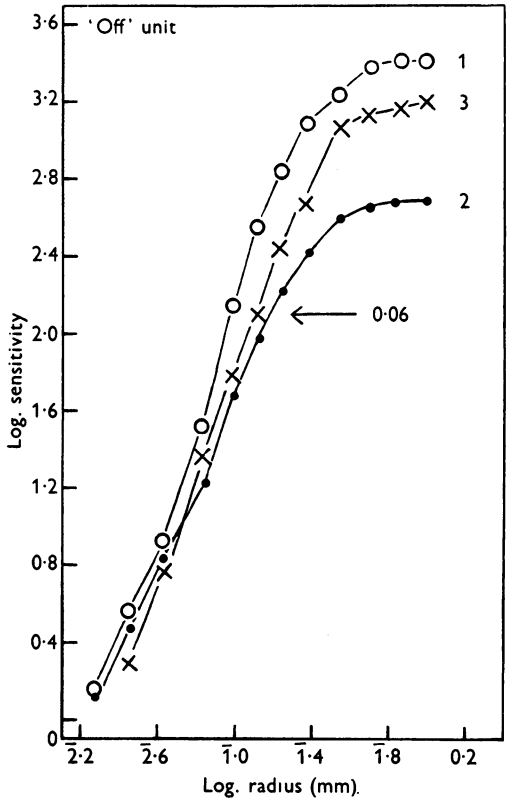

Fig. 6. Observed radius/sensitivity relation (1 and 3), and relation calculated from map of receptive field (2) in an 'off' unit.

a radius of about 0·2 mm; this might correspond to the point at which the spot starts to encroach on the less sensitive peripheral fringe of the receptive fields. This amounts to the hypothesis that the sensitivity observed when any region of the retina is illuminated at a uniform intensity will be the sum of the sensitivities of the small parts of the retina included in the region illuminated. If this was so, the area/sensitivity relation of Fig. 5 should be predictable from a complete map of the sensitivity in the receptive field.

Fig. 6 shows an experiment designed to test this. First the centre of a well isolated unit was located, then the threshold for the series of stimuli of different sizes centred on this point was determined (curve 1). A complete

map of the receptive field was next made, using a spot 0·133 mm in diameter moved in steps of 0·114 mm. The complete area/threshold set was then repeated (curve 3). From the map of the receptive field the sensitivities for spots of different sizes was calculated by drawing a circle of appropriate size on the map, and adding up the sensitivities of the regions included. It was assumed that sensitivity was proportional to area for spots below the size of the exploring spot, and for fractional areas included by spots of larger size. This is shown in Fig. 6 (curve 2) and it will be seen that the observed sensitivities exceed the calculated one by quite a wide margin with spots of large size, but with small spots the agreement is satisfactory. The observed and calculated curves bend over at very nearly the same values, indicating that the assumption that this flattening is caused by the stimulus spot first spreading to the fringe of reduced sensitivity, and then right off the receptive field, is probably correct.

The discrepancy between observed and calculated sensitivity with large spots appears to be genuine. Only two experiments of this type have been successfully completed because they require about 3 hr, and only a small proportion of preparations last as long as this. The other successful one showed a slightly smaller discrepancy, and there has been evidence of it in incomplete experiments. There are, of course, innumerable modifications of the original assumptions which would enable one to obtain a fit well within experimental error, but there is no experimental or theoretical evidence to decide which is appropriate. Empirically it is found that calculations based on the assumption that the effects contributed to the ganglion cell are not strictly proportional to intensity of light but to the 0·83 power of intensity, give a remarkably good fit over the whole range of values The assumption of linear addition can also be modified to yield the same result.

These experiments show that an 'off' ganglion cell summates subliminal effects contributed from all its receptive field, but there is evidence either that the effects are not quite proportional to intensity, or that the summation is not quite linear.

'On-off' units, It is immediately obvious from the results shown in Fig. 5 that 'on-off' units possess an inhibitory, or subtracting, mechanism in addition to the summating mechanism found in 'off' units; there is no other explanation for the fact that adding an annulus to the stimulus spot reduces the sensitivity The experiments described here were designed to clarify this effect.

Fig. 7 shows for an 'on-off' unit an experiment of the type just described for 'off' units. Curves 1 and 3 are the observed sensitivities determined before and after the mapping of the receptive field. Curve 2 is the sensitivity calculated from the map on the basis of linear summation of sensitivities. The divergence between the two experimental curves is uncomfortably large, but the main points stand out clearly enough. There is nearly complete summation

for spots below 0·1 mm radius. From this point onwards the experimental points lie below the calculated points, and from 0·4 mm radius onwards the sensitivity decreases as the spot size increases. It will be seen from curve 2 that the maximum sensitivity occurs when the spot just covers the receptive field, but does not overlap the surrounding retina. When the surrounding retina is excited together with the receptive field, the sensitivity is decreased.

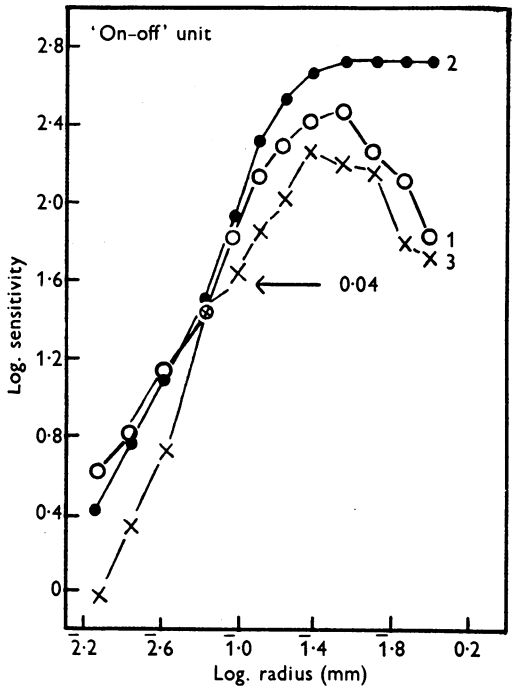

Fig. 7. Observed radius/sensitivity relation (1 and 3), and relation calculated from map of receptive field (2) in an 'on-off' unit.

This shows that the inhibitory effect is elicited by light falling on that part of the retina which immediately surrounds the receptive field of the 'on-off' unit; if a portion of retina has an excitatory action on the ganglion cell (i.e. lies within the receptive field) it does not have an inhibitory action when other parts are excited with it. The observed sensitivity is less than the calculated sensitivity (in contrast to the 'off' units) when the spot is large but lies entirely within the receptive field, and the reason for this is not clear.

Other experiments of this type confirm these conclusions. In particular, the maximum observed sensitivity was always lower than the maximum calculated sensitivity, but decreasing sensitivity did not occur until parts of the retina lying outside the receptive field were illuminated. Some experiments on 'on-off' units did not show the decrease of sensitivity at large spot sizes,

but in these cases the unit often gave only an 'on' or an 'off' response with a large spot, whereas a smaller centrally-located spot gave both at threshold intensities. It was usually the custom to measure only the lower of the two thresholds (for 'on' or for 'off') in order to avoid fatiguing the preparation, and it is possible that the higher of the two thresholds would have increased more at large diameters. Fig. 8 shows an 'on-off' unit in which both thresholds were measured. In this case the 'off' response had a lower threshold

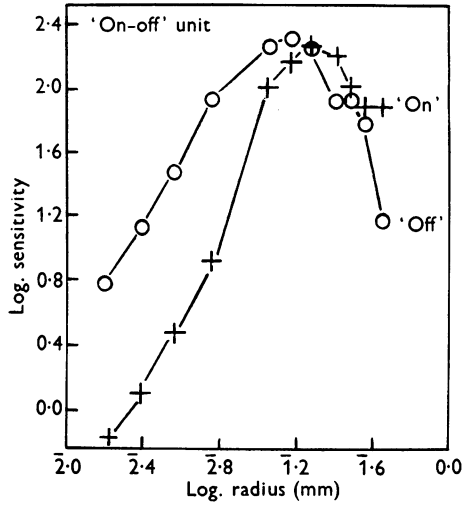

Fig. 8. Radius/sensitivity relation for 'on' (crosses) and 'off' (circles) responses in an 'on-off' unit.

with small spots, they had about the same threshold for medium-sized spots, and the 'on' threshold was lower with large spots. This complex type of behaviour has not been further analyzed, but it is probably related to the results shown in Figs. 4 and 11.

The existence of the inhibition is shown more directly by the experiment illustrated in Fig. 9. One spot of light was centered on the receptive field, and adjusted in intensity until it always gave a volley of impulses both when the light was switched on and when it was switched off. A second spot, turned on and off with the first, was then placed about 1 mm from the centre of the receptive field; it was at an intensity 1000 times above its threshold, measured when it was located on the centre of the receptive field, but when moved off to the point 1 mm away it gave no response at this level, nor at any lower level. Fig. 9 shows the result of turning both spots on and off together, and the result of turning the central spot on and off alone. The peripherally-placed spot clearly decreases the discharge elicited by the centrally-placed spot, and the suspected inhibition is shown directly.

Summation within the receptive field was found to approximate to the

linear addition of subliminal effects from all over the receptive field, the amount contributed by each part being approximately proportional to its sensitivity and to the intensity of light falling on it. The next experiments were designed to see if the inhibitory phenomenon approximated to the subtraction of an effect proportional to the intensity of the light. Two spots of

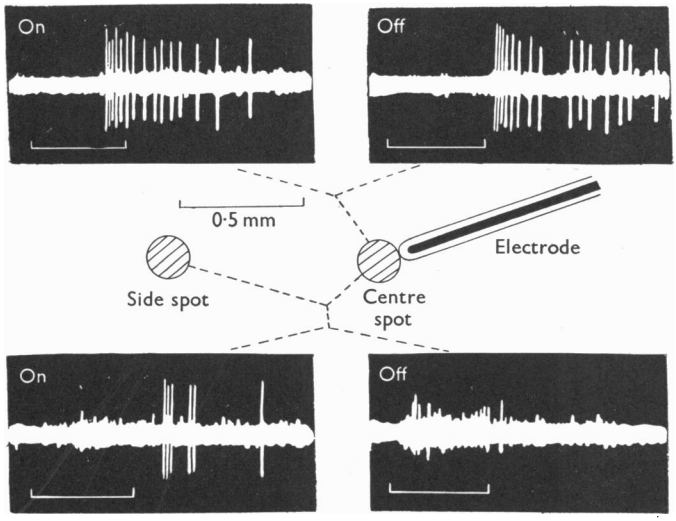

Fig. 9. Discharge produced by central spot inhibited by side spot turned on and off with it. Top: centre spot alone. Bottom: centre and side spots. Time marked on records, 0·2 sec.

light, one in the receptive field, and the other in the inhibitory fringe, were turned on and off together; the threshold intensity of the central (excitatory) spot was measured with the peripheral (inhibitory) spot at different intensities.

Fig. 10 shows the result of such an experiment. The central spot was the 0·067 mm radius spot normally used for exploring the receptive fields. The peripheral spot was the side-light of the stimulator (see Barlow, 1952), and was the image of an electric filament which measured $0{\cdot}3 \times 0{\cdot}04$ mm on the retina; this was first placed centrally on the receptive field and the threshold determined. It was then moved to a point 0·7 mm from the centre. This peripherally-placed spot was turned on and off together with the centrally-placed one, and the threshold was determined by adjusting the intensity of the central spot. Thresholds were determined with the side spot set to deliver stimuli of intensities up to 1000 times the intensity required to excite when the side spot was centrally placed, but by itself it never produced a response when peripherally placed. The ordinates are the threshold intensities of the centre spot plotted as a multiple of its 'off' threshold without the other spot. The abscissae are the intensities of the side spot, plotted as a multiple of the

'off' threshold intensity of this spot when it was centrally placed. The lines are drawn through the points for the 'off' response, one run being done in each direction. The errors for the upper points are large, but a straight line of slope 0·011 gives a reasonable fit.

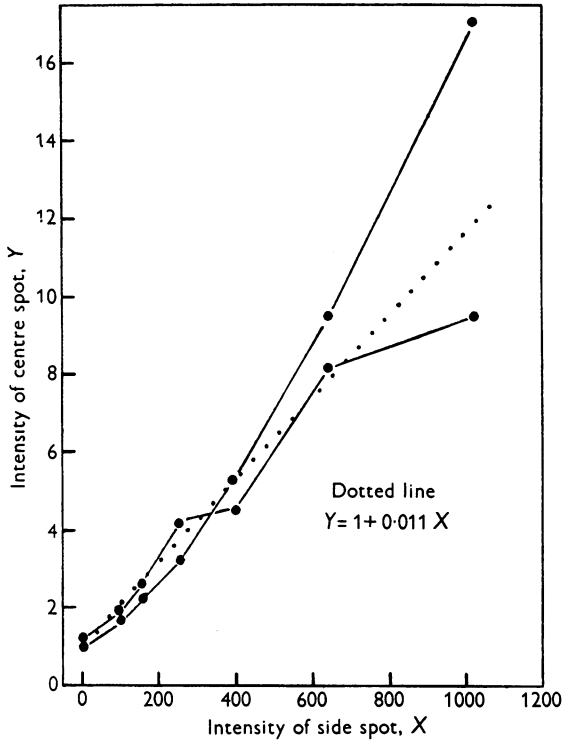

Fig. 10. Threshold intensity of centre spot (Y), as multiple of its threshold alone, plotted against intensity of side spot (X) expressed as multiple of its threshold when it is centrally placed. 'On-off' unit, off response. Side spot is 0·7 mm from centre of receptive field.

If Y is the quantity plotted as ordinate, and X the quantity plotted as abscissa, then $Y=1+0{\cdot}011X$, or $Y-0{\cdot}011X=1$, expresses the threshold condition of this ganglion cell under these particular conditions. This corresponds to the linear subtraction of a quantity proportional both to the intensity of the light and to a quantity which might be defined as 'inhibitory sensitivity'. An 'inhibitory sensitivity' thus behaves like a negative sensitivity, and it could then be said that the sensitivity of a ganglion cell declines to zero at the edge of its receptive field, and then assumes negative values. The actual value of the negative sensitivity observed at 0·7 mm from the centre of the receptive field in this experiment is of the right magnitude to account for the decrease of sensitivity with large spots observed in the area/threshold experiments.

Fig. 11 shows an experiment similar to the last one, in which the threshold for both 'on' and 'off' responses was measured. It will be seen that there was about the same amount of inhibition of the 'off' response by the peripheral spot, but a very much smaller inhibition of the 'on' response. Such a ganglion cell gives practically no 'off' response to a large stimulus, because it is almost completely inhibited by the light falling on the inhibitory fringe, but the 'on' response is vigorous because it is not inhibited. The results of these experiments on 'on-off' units can be summarized by saying that, as well as the summating properties of 'off-units', they possess an inhibitory, or subtracting, mechanism actuated by light falling outside the receptive field.

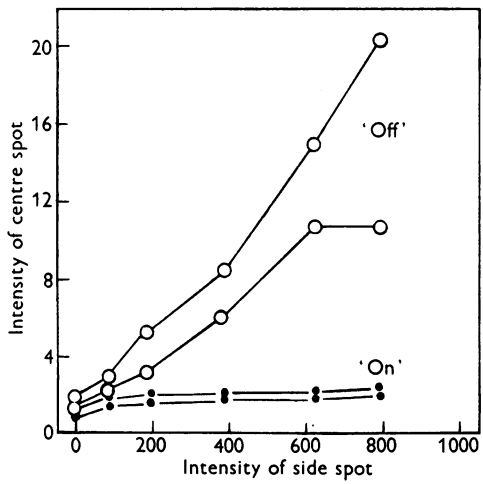

Fig. 11. 'On-off' unit, both responses. Side spot displaced 0·8 mm. Ordinates and abscissae as in Fig. 10. The 'off' response is more powerfully inhibited than the 'on' response.

Movement sensitivity

There is an easily detectable difference between the responses of 'off' and 'on-off' units to moving stimuli. The 'off' units discharge whenever the total amount of light reaching the receptive field is reduced. This can be done by turning off, or reducing the intensity of, a patch of light that covers the whole or part of the receptive field, or by moving a spot of light into a less sensitive region, or by moving a darker patch onto a more sensitive region; the resulting discharges are always similar, though they are more prolonged if the stimulus is prolonged by, for example, slowly and continuously reducing the intensity of illumination. This type of behaviour is exactly what one would expect if the 'off' type of ganglion cell responds only to the summated effects of light falling all over the receptive field, and is unable to differentiate in any way between the contributions from the different parts. The same is not true of 'on-off' units These respond to all the types of stimulation already mentioned, and also to the

opposite types which result in an increase in the summated amount of light in the receptive field; but they also respond to a change in the spatial pattern of light even if this does not alter the total amount of light falling on the receptive field. It is difficult to be sure that this is so, for it is not easy to find even a limited region of the receptive field within which the sensitivities to both 'on' and 'off' are constant, but occasionally both are fairly constant, and even then an 'on-off' unit will respond vigorously to movement of a small spot of light within this region if it is only a few times threshold intensity. Any attempt to explain this behaviour would require an analysis of the temporal characteristics of excitability, and this has not been attempted; it was observed qualitatively that there was great variability in the rate of adaptation of supra-threshold discharges elicited by a small stimulus in 'on-off' units, whereas discharges of 'off' units always adapted at about the same rate. This, together with the fact that there is both an 'on' and an 'off' discharge and the thresholds for each tend to vary even in the central plateau, may account for the greater movement sensitivity of 'on-off' units.

DISCUSSION

The results described are in good agreement with those of Hartline. The receptive fields of the units isolated by this technique measure up to 1 mm in diameter in the periphery of the frog's retina. The region of high sensitivity in the centre of the receptive field is smaller, about 0·5 mm in diameter. Some indication was obtained that the receptive fields of units lying in the more central regions of the retina are smaller, but it was, unfortunately, very difficult to isolate the more central units. The reason for this is not clear, but it may simply be that the layer of nerve fibres, which is denser near the optic disc, prevents the electrode from approaching close enough to the ganglion cell.

Reasons have been given elsewhere (Barlow, 1952) for believing that the units isolated by this technique in the frog do not belong to any particularly rare or unusual class of ganglion cell. If this is accepted, then each receptive field must overlap with about eighty other receptive fields. Because it is uncertain that the potentials are from typical units, one is on safer ground when talking about convergence. Simply from the numbers of ganglion cells and receptor cells, there must be at least a 30 to 1 convergence; in fact it appears that the units isolated pick up from a region containing 2000 receptors, though it cannot be shown that all of these receptors connect functionally with the ganglion cell.

The experiments showing summation of subliminal effects from all over the receptive field confirm the conclusions that could be drawn from indirect experiments such as those of Adrian & Matthews, and the direct ones of Hartline. It is very remarkable that a simple nervous structure, consisting of

a single ganglion cell connecting through bipolar cells with a number of receptor cells, can perform an addition sum with tolerable accuracy. The smallest spots in the area/threshold experiments are illuminated at an intensity 1000 times higher than the largest spots, and it therefore appears that the effects contributed by the receptors can be graded over this very large range. At first sight it appears most unlikely that this could be done by the transmission of all-or-nothing impulses, but there are two considerations which make it less unlikely. In the first place, nothing whatever is known about the relation between the quantity which is transmitted and the intensity of the light. It is true that the quantity which is summated is approximately proportional to the light intensity, but this could be so for many functional relations between intensity and transmitted quantity if the inverse operation was performed before the quantities were added. Secondly, one could account for the summation on a hypothesis involving probabilities; this is perhaps best illustrated by an example. If a cell discharges when ten impulses reach it along any of, say, 1,000,000 possible channels, and if the probability of an impulse arriving along any single channel is directly proportional to the intensity of light falling on the part of the retina it comes from, then the observed behaviour would be accounted for. Clearly one cannot make any progress without being able to observe activities in structures lying between the ganglion cell and the receptors.

The inhibitory action of light falling outside the receptive field of 'on-off' fibres has not been described before. It is not surprising that it has not been observed in threshold experiments on man, for any units which were uninhibited would have lower thresholds, and would therefore be responsible for the threshold. Simultaneous contrast effects are presumably caused by an inhibitory mechanism similar to the one described; a white spot surrounded by black looks brighter (more impulses) than a white spot of the same intensity surrounded by grey, because the grey falls on the inhibitory fringe of the ganglion cells, and so inhibits their discharge (causes fewer impulses).

Hartline did not observe inhibition because his stimulus spots did not extend outside the receptive field. It may, however, be related to the inhibition he observed at high intensities. He found that the number of impulses increased with intensity at low intensities; it then reached a maximum, after which the number of impulses decreased with further increase of intensity. This could be accounted for by the excitatory mechanism from the receptive field overloading, or failing to respond linearly, at a lower intensity than the inhibitory mechanism. It is probably also related to the various forms of temporal inhibition postulated by Granit (1947); his experiments were done with large stimuli which would cover both excitatory and inhibitory regions of the retina, and the results he observed would represent the excess of the excitatory over the inhibitory process. He distinguished between them by

their temporal characteristics and there is at least a chance that all the inhibitory effects result from light falling outside the receptive field.

There are, however, some facts which show that the 'on-off' units are more than simple 'off' units with an additional inhibitory mechanism. In the first place they discharge at 'on' as well as 'off'; secondly, they do not summate completely over large areas (compare Fig. 7 and Fig. 6); and thirdly, they have a greater sensitivity to movement than could be accounted for on this idea. The fact that they can resolve movement within their receptive fields helps to explain the paradoxical combination of an efficient optical system producing a sharp optical image and overlapping receptive fields producing a 'blurred' pattern of activity in the optic nerve: clearly the sharp optical image may help in the detection of movement within the receptive field.

The type of discrimination achieved by the 'on-off' units is also interesting in considering colour discrimination. The 'on-off' unit connects to the receptors in such a way that moving a light from one lot of receptors to another in a different part of the receptive field causes a discharge. If it makes analogous connexions to receptors which differ, not in position, but in spectral sensitivity, then it would discharge when the colour of a light was changed. This would be useful, for it would enable a moving object to be detected when it only differed from the background in colour, and it would be a true colour discrimination, for it would hold for all relative intensities of the two colours, but it would be missed in behaviour experiments of the conditioned reflex type designed to detect colour vision.

There is a great deal of convergence from the level at which light is detected to the level at which the resulting neurological activity is transmitted back to the central nervous system. In Sherringtonian language, an optic nerve fibre is the final common path for activity aroused over a considered region of the retina, and if some purposive integration has taken place it should be possible to relate this to the visual behaviour of the frog. According to Yerkes (1903), the frog uses its eyes mainly in feeding; it also escapes from large moving objects, but it does not use visual cues in orientating itself in its habitat. When feeding, its attention is attracted by its prey, which it will approach, and finally strike at and swallow. Any small moving object will evoke this behaviour, and there is no indication of any form discrimination. In fact, 'on-off' units seem to possess the whole of the discriminatory mechanism needed to account for this rather simple behaviour. The receptive field of an 'on-off' unit would be nicely filled by the image of a fly at 2 in. distance and it is difficult to avoid the conclusion that the 'on-off' units are matched to this stimulus and act as 'fly detectors'.

It was shown previously that 'off' units are most frequently found in the posterior retina. This is the retinal region on which the image of a fly will fall when the frog has located it and turned towards it. The frog now needs

accurate information about the exact position of the fly, and it is possible that the 'off' units are adapted to do this. At first sight one is inclined to think that a large receptive field would be unsuitable for locating objects accurately, but this is only so if one is considering objects whose image on the retina is smaller than the receptive field. A population of ganglion cells with over-lapping receptive fields of the same size as the expected image is a neat method of judging the centre of a large object, for there will be a single, unique, ganglion cell whose field is completely filled by the image, and which will, therefore, be maximally excited; if the receptive fields were either larger or smaller there would be several ganglion cells completely enclosing, or completely covered by the image. A dark fly 6 mm long at a distance of 2 in. would give an image exactly filling a receptive field 0·3 mm in diameter in a frog with posterior nodal distance 2·5 mm and this fits in with the idea that off units are position indicators for flies darker than their backgrounds. There is one other property of 'off' units which is worth pointing out. If a fly is moving, the greatest 'off' activity will lie ahead of the centre of the fly's image on the retina, for the illumination of receptive fields of ganglion cells in front of the fly will be decreasing, whereas, for those behind it, it will be increasing. Hence the region of greatest 'off' activity indicates the future position of the fly, not its present position. This would help to compensate for the reaction time of the frog, but it is doubtful if the compensation would be exact, except under very special conditions.

Perhaps the idea of sensory integration has been pressed too far, but the distortions introduced by the retina seem to be meaningful; the retina is acting as a filter rejecting unwanted information and passing useful information.

SUMMARY

1. Units isolated by Granit's technique in the isolated frog's retina have receptive fields with a central plateau, of high sensitivity 0·2–0·6 mm in diameter.

2. In some units the sensitivities for 'on' and 'off' responses are not similarly distributed.

3. 'Off' units summate subliminal stimuli over the whole of their receptive fields, but are unaffected by light falling outside it.

4. 'On-off' units summate subliminal stimuli over their receptive fields, but rather less completely than 'off' units. Light falling outside the receptive field has an inhibitory action.

5. The amount of inhibition produced, measured by the rise in threshold of a central spot of light, is proportional to the intensity of the light falling outside the receptive field.

6. The amount of inhibition is often different for 'on' and 'off' responses in an 'on-off' unit. There is no such inhibition in pure 'off' units.

7. Possible functions, related to the visual behaviour of the frog, are suggested for 'off' and 'on-off' units.

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